Host locating behaviour of Leschenaultia exul and Patelloa pachypyga: two tachinid parasitoids of the forest tent caterpillar, Malacosoma disstria

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Abstract

Leschenaultia exul (Townsend) and Patelloa pachypyga (Aldrich & Webber) (Diptera: Tachinidae) are the principal larval parasitoids of the forest tent caterpillar (FTC) Malacosoma disstria (Hübner) (Lepidoptera: Lasiocampidae) in Canada. The response of these two fly species to M. disstria differs depending on the tree species on which the host feeds. In wind tunnel experiments, L. exul spent more time on the side of the tunnel containing volatiles from FTC frass and was attracted to the FTC-aspen poplar (Populus tremuloides Michx.) complex preferentially to the FTC-balsam poplar (Populus balsamifera L.) complex. Field bioassays confirmed that this fly species was preferentially attracted to the herbivore-aspen poplar complex as compared to the herbivore-balsam poplar complex. In field bioassays, P. pachypyga was also attracted preferentially to aspen poplar trees containing FTC larvae, compared to balsam poplar trees with host larvae.

Introduction

The forest tent caterpillar (FTC), Malacosoma disstria (Hübner), is a significant defoliator of forest trees in North America (Hodson, 1941). Although the principal host tree is aspen poplar, Populus tremuloides Michx., at high caterpillar densities the larvae will feed on many other tree and shrub species including balsam poplar, birch, alder, willow, and rose. Outbreaks of this insect are, in part, suppressed by natural enemies such as parasitoids, viral pathogens, and various predators (Witter & Kulman, 1972, 1979). In Canada, the predominant parasitoids attacking late-instar FTC larvae are the tachinids Leschenaultia exul (Townsend) and Patelloa pachypyga (Aldrich & Webber) (Sippell, 1957; Parry, 1994).

Leschenaultia exul is a specialist parasitoid, parasitizing only three species of Malacosoma larvae: M. americanum (Fabricius), M. disstria, and M. pluviale (Dyar) (Sippell, 1957; Arnaud, 1978). Patelloa pachypyga is even more restrictive, normally parasitizing only M. disstria (Sippell, 1957; Witter & Kulman, 1972; Arnaud, 1978). Both of these tachinids parasitize up to 50% of late instar larvae in aspen feeding populations (Sippell, 1957; Witter & Kulman, 1979; Roland & Taylor, 1995). However, these percentages can vary greatly among years and locations (Bess, 1936; Parry, 1995).

Leschenaultia exul and P. pachypyga do not attack FTCs directly but, instead, lay eggs on damaged foliage near feeding host larvae (Bess, 1936; O’Hara, 1985). Eggs are ingested by the host and hatch inside the host’s gut. Neonate maggots move to the host’s salivary glands, and then migrate to the haemocoel where they complete development (Bess, 1936; O’Hara, 1985). Fully developed maggots emerge from the host, drop to the ground, and pupate beneath the host tree where the adult flies emerge the following spring. Host-finding may therefore seem superfluous since these parasitoids pupate and subsequently emerge from beneath the host tree. However, the host redistributes itself through dispersal of the adult female moths and, in the 10–14 day
previposition period, female parasitoids travel to other locations to feed on nectar and to mate (Herrebout, 1967).

To locate host larvae, parasitoids rely on a variety of cues arising from either the herbivore and/or their host plants (Vet & Dicke, 1992). Cues arising directly from herbivores or their by-products (e.g., frass) are more reliable indicators of larval presence than are cues arising from their host plants. Host plant stimuli are easier to detect in a large, heterogeneous environment due to the larger size of the host plant compared to the herbivore. This reliability-detectability trade-off (Vet & Dicke, 1992) may explain why different parasitoid species use a wide range of stimuli, both visual and olfactory, and emanating from either the herbivore or host plant.

*Leschenaultia exul* females oviposit on wild cherry trees near feeding tent caterpillar larvae (Bess, 1936), and *L. exul* will land on aspen poplar leaves adjacent to feeding caterpillars (Sippell, 1957). Nothing is known of *P. pachypygna* searching behaviour. It is unknown whether *L. exul* and *P. pachypygna* are attracted to the host caterpillar or the host’s primary food plant (aspen poplar). It is also unknown whether the two parasitoid species are attracted to host-feeding only on aspen poplar or on other plant species. Leaf-ovipositing tachinids, such as *Cyzenis albicans* (Fall.), are known to be attracted to odours from caterpillar-damaged host plants but not from damaged non-host plants (Roland et al., 1989; Roland et al., 1995). It was therefore our intention to determine the stimuli attracting *L. exul* and *P. pachypygna* to FTC larvae.

**Materials and methods**

To assess the response of *L. exul* to host habitat stimuli we used both wind tunnel choice experiments, for visual and olfactory stimuli, and field bioassays of fly attraction to host trees with varying levels of FTC larvae and host plant defoliation. *Patelloa pachypygna* were not easily maintained in the laboratory and were, therefore, only studied using field bioassays.

**Wind tunnel bioassay**

*Insects.* Adult *L. exul* were collected on 10 May 1994 from aspen forests at Ministik Hills (113°00’W, 53°22’N), approximately 30 km east of the city of Edmonton, Alberta, Canada. Forest at this site consists mainly of aspen poplar, *P. tremuloides* interspersed with, in descending order of abundance, balsam poplar, *P. balsamifera*, paper birch *Betula papyrifera* Marsh., and white spruce *Picea glauca* (Moench) Voss (Roland & Taylor, 1995). Trees at this site showed a range of FTC defoliation from light to extremely heavy.

Flies were collected when they were either mating on exposed substrates such as fallen logs, roads, tall grass in clearings, or while nectar feeding on buffaloberry, *Shepherdia canadensis* (L.) Nutt. Flies were maintained for 16 days in a controlled environment chamber at 23 °C during the day and 13 °C at night, with a corresponding photoperiod of L16:D8, and a r.h. of 60%, which simulated natural temperature and photoperiod. Flies were fed fresh honey, powdered milk, sugar, and water *ad libitum*. Males and females were caged together to ensure that females were mated and gravid.

Caterpillars were collected from aspen poplar foliage at the same field site. FTCs were maintained in the laboratory and supplied fresh aspen foliage daily. Aspen poplar and balsam poplar foliage used in the bioassays were collected from an area with no FTC outbreaks for the last eight years. The foliage, therefore, had no FTC feeding damage and no parasitoid eggs.

**Bioassay.** The flies’ responses to test items were evaluated in a variable-speed wind tunnel. The tunnel was 50 cm × 50 cm in section, and 200 cm in length and was made of clear Plexiglas. Air was drawn through the tunnel at 0.3 m/s. The floor of the tunnel was lined with medium brown paper held down with large stones to provide the flies with reference points while flying towards test items. All wind tunnel testing was performed between 0800 and 1700 h to avoid testing flies at times when they would not normally be active (Bess, 1936).

Nineteen flies were selected at random and presented with each of the following paired choices:

(a) Undamaged aspen leaves vs. undamaged balsam leaves. Even though both tree species are fed on by caterpillars, aspen is the preferred host plant. Flies should not be attracted to leaves without feeding damage, as this would be an inefficient host-finding strategy.

(b) Aspen leaves with FTC feeding damage vs. aspen leaves with mechanical damage. Herbivore-damaged plants can emit specific chemical cues indicating the presence of larval feeding damage, while mechanical damage releases non-specific chemical cues (Turlings et al., 1993). Both types of damage look similar, so
this pairing evaluates the importance of insect-caused damage.

(c) FTCs eating aspen leaves vs. FTCs eating balsam leaves. Aspen is the preferred host plant of the FTC. Therefore, *L. exul* should be attracted to volatile cues emanating from larval-damaged aspen leaves. By having the same number of caterpillars on the two tree species we measured the parasitoids attraction to only volatile olfactory stimuli from each of the two plant-herbivore complexes, as larval stimuli alone would not differ between the two choices.

(d) FTCs only vs. model FTCs. Olfactory cues from host insects are potentially attractive to tachinid flies. We compared real caterpillars to model caterpillars. Model caterpillars were made from small paper tubes 4 cm long × 1 cm in diameter to mimic FTC coloration. The visual stimuli between the real and model caterpillars were similar but olfactory cues would differ.

(e) FTC frass vs. wet sand. Caterpillar frass contains modified host plant compounds and could be a powerful olfactory cue for attracting *L. exul*. We compared the attractiveness of frass to wet sand. Because the sand looked like frass, the main difference between the two items would be olfactory cues.

For each set of paired choices, plant specimens were placed in water-filled 500 ml glass jars (jars were covered with brown paper to eliminate any possible visual attraction to water) and then placed in the wind tunnel. Real FTCs, model FTCs, frass, and sand were all placed in 10 cm Petri dishes set on the top of the glass jars in the upwind section of the wind tunnel.

Pairs of test items were located on separate sides, in the farthest upwind section of the wind tunnel. For each test, one fly was introduced through a hole in the top of the downwind section of the tunnel. Each fly was then permitted 25 min of searching. At 1, 2, 5, 10, 15, 20, and 25 min after the fly had entered the wind tunnel, the quadrant in which it was located (left – right, upwind – downwind) was recorded. At the end of each 25 min test, the fly was removed from the tunnel and the wind tunnel was allowed to exhaust residual odours for 5 min while another pair of test items were placed in the tunnel. The same fly was then exposed to this pair of test items. This procedure continued until each fly was exposed to all pairs of test items. Pairs of test items were presented to the flies in random order and the positions of the paired items were alternated between sides of the tunnel in each set of tests.

### Statistical analyses

Two sets of data were analyzed:

1. which side of the wind tunnel (treatment vs. ‘control’) flies aggregated on, even if the flies did not move upwind, and
2. for those flies that did move upwind, which side of the wind tunnel (treatment vs. ‘control’) was preferred. The proportion of time each fly spent on the treatment vs. control side of the wind tunnel was compared by assigning either a ‘+’ if more time was spent on the treatment side and assigned a ‘−’ if more time was spent on the ‘control’ side. The number of pluses and minuses were compared using the nonparametric Sign test.

### Field bioassay

**Bioassay and experimental design.** Fly behaviour was observed in the canopies of small aspen poplar (*n* = 48) and balsam poplar (*n* = 44) trees, with varying levels of defoliation and host caterpillar abundance. Observations were conducted in the same area from which flies were obtained for the wind tunnel experiments. The total number of FTCs was recorded and the approximate percent defoliation of each tree canopy was recorded. The total number of *L. exul* and *P. pachypyg* landing on the tree canopy was recorded during a 15 min interval. *Leschenaultia exul* were easily identified due to their large size and characteristic zigzag flight pattern. In flight, *P. pachypyg* were difficult to distinguish from *Arachnidiomyia aldrichi* (Park- er) (Diptera: Sarcophagidae) except that *P. pachypyg* have much darker eyes than do *A. aldrichi*. These two species were easily distinguished once they had landed on the tree.

Observations alternated between aspen poplar and balsam poplar trees. No tree was used more than once. Data were collected on four days between 30 May and 8 June 1995 between 0800 and 1700 hours.

**Statistical analyses.** A random sample of the field trees used for observational bioassays were selected for height (indicative of overall size) comparisons, using a *t*-test. Levels of defoliation and host caterpillar abundance for all aspen and balsam poplar field trees were compared using non-parametric Mann–Whitney *U*-tests. The number of flies landing on aspen and balsam poplar tree canopies was compared using a chi-square test. In addition, for each fly species simple regressions were performed to estimate the effects of percent defoliation of tree canopy (arcsin transformed) and FTC larval abundance on the number of flies attracted to aspen and balsam poplar trees.
Figure 1. Number of *L. exul*: (a) on the side of the wind tunnel containing each paired choice item, and (b) flying upwind, in response to stimuli from paired-choice items. (L) and (R) indicate left and right columns, respectively, within each choice test (not the side of the wind tunnel). Within each choice test, columns labelled with different letters are significantly different from each other (Sign test $P < 0.05$).

**Results**

**Wind tunnel bioassay**

There was no difference in the number of *L. exul* on the side of the wind tunnel containing undamaged aspen poplar leaves versus undamaged balsam poplar leaves (Figure 1a, $P = 0.36$). No difference was found in the number of flies on the side with caterpillar damaged aspen poplar leaves compared to mechanically damaged aspen leaves ($P = 1.00$), nor between real caterpillars versus model caterpillars ($P = 1.00$). There were, however, more flies on the side of the wind tunnel with caterpillars actively feeding on aspen poplar leaves compared to the side with caterpillars eating balsam poplar leaves ($P = 0.019$). Flies also preferred the side of the wind tunnel containing caterpillar frass (from aspen poplar) compared with wet sand ($P = 0.019$) (Figure 1a).

Among *L. exul* that moved upwind, the same patterns were apparent (Figure 1b). There was no significant difference between undamaged aspen poplar leaves and undamaged balsam poplar leaves ($P = 0.55$). No difference was found between caterpillar damaged aspen poplar leaves and mechanically damaged aspen poplar leaves ($P = 1.00$). Flies responded to damaged aspen poplar leaves in preference to damaged balsam poplar leaves ($P = 0.012$). No difference was found between live FTCs versus model FTCs ($P = 1.00$). However, unlike the previous analysis, there was no difference in attractiveness between frass and wet sand ($P = 0.22$) (Figure 1b).

**Field bioassay**

Aspen and balsam poplar trees did not differ significantly in height ($t = -0.51$, df = 28, $P = 0.622$). The two species of field trees did differ with respect to larval abundance ($U = 374$, $P = 0.0001$) and defoliation levels ($U = 400.5$, $P = 0.0001$), with aspen poplar trees having significantly greater values for both factors compared to balsam poplar trees (Table 1).
Table 1. Height, larval abundance, and defoliation comparisons of trees selected for field attraction studies

<table>
<thead>
<tr>
<th>Tree Species</th>
<th>Aspen Poplar</th>
<th>Balsam Poplar</th>
</tr>
</thead>
<tbody>
<tr>
<td>Height(^1)</td>
<td>Range 1.6–4.55 m (mean = 2.965, s.e. = 0.210) (^a)</td>
<td>Range 2.2–4.65 m (mean = 3.135, s.e. = 0.217) (^a)</td>
</tr>
<tr>
<td>Larvae(^2)</td>
<td>Range 0–300 (mean = 53.33, s.e. = 7.921) (^a) (Median = 40.00)</td>
<td>Range 0–100 (mean = 9.818, s.e. = 2.945) (^b) (Median = 0.00)</td>
</tr>
<tr>
<td>Defoliation(^2)</td>
<td>Range 0–63.435 (mean = 27.57, s.e. = 2.617) (^a) (Median = 30.0)</td>
<td>Range 0–30.0 (mean = 7.74, s.e. = 1.406) (^b) (Median = 0.00)</td>
</tr>
</tbody>
</table>

Means followed by different letters within a row are significantly different (\(P < 0.05\)):
\(^1\) Determined by a two sample, two tailed \(t\)-test.
\(^2\) Determined by a Mann–Whitney \(U\)-test.

Means followed by different letters within a row are significantly different (\(P < 0.05\)).

Figure 2. Number of \(L.\ exul\) and \(P.\ pachypsyga\) flies landing on aspen poplar and balsam poplar tree canopies during 15 min field observations. For each fly species, columns labelled with different letters are significantly different from each other (\(\chi^2\) test \(P < 0.05\)).

Significantly more \(L.\ exul\) were attracted to the canopies of aspen poplar trees compared to the canopies of balsam poplar trees (\(\chi^2 = 7.143, df = 1, P = 0.0075\)) (Figure 2). There were also significantly greater numbers of \(P.\ pachypsyga\) flies landing on aspen poplar tree canopies compared to balsam poplar tree canopies (\(\chi^2 = 16.333, df = 1, P = 0.0001\)) (Figure 2).

On aspen poplar trees, more \(L.\ exul\) entered tree canopies with higher numbers of caterpillars (\(P = 0.0225\)). Overall level of defoliation was not a good predictor of the number of \(L.\ exul\) landing on aspen poplar tree canopies (\(P = 0.5439\)). On balsam poplar trees, neither larval abundance (\(P = 0.4734\)) nor overall level of defoliation (\(P = 0.2336\)) was a good predictor of the number of \(L.\ exul\) landing on the tree canopies. In fact, on balsam poplar trees there were negative relationships for both variables, i.e., as the number of larvae and defoliation increased, fly attraction decreased (Table 2). For \(P.\ pachypsyga\), on aspen poplar trees neither larval abundance (\(P = 0.1939\)) nor overall level of defoliation (\(P = 0.8838\)) were significant factors predicting fly attraction. On balsam poplar trees both larval abundance (\(P = 0.162\)) and overall level of defoliation (\(P = 0.1721\)) were non-significant, but both had negative correlations with fly attraction (Table 2).

Discussion

Natural selection is expected to favor plants that attract parasitoids, while it would minimize the release of chemical cues from host larvae (Dicke & Sabelis, 1988). Based on our experiments and observations, \(L.\ exul\) and \(P.\ pachypsyga\) do not respond to cues directly from FTCs, but these parasitoids do respond to cues from herbivore by-products (i.e., frass) and larval damage on the FTCs’ principal food plant, aspen poplar trees.

The only stimulus that attracted \(L.\ exul\) was the FTC-aspen poplar complex. In laboratory experiments, the effect of the host on the host plant appeared to be synergistic, as flies were not attracted to FTCs or to
Table 2. Simple regression analysis of *Leschenaultia exul* and *Patelloa pachypyga* attraction to aspen and balsam poplar trees, using larval abundance and level of defoliation as variables

<table>
<thead>
<tr>
<th>Tree species</th>
<th>Variable</th>
<th>Coefficient</th>
<th>$R^2$</th>
<th>P value*</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Leschenaultia exul</em>:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aspen</td>
<td>Larvae</td>
<td>0.0032</td>
<td>0.108</td>
<td>P &lt; 0.05</td>
</tr>
<tr>
<td></td>
<td>Defoliation</td>
<td>0.0026</td>
<td>0.008</td>
<td>NS</td>
</tr>
<tr>
<td>Balsam</td>
<td>Larvae</td>
<td>-0.0012</td>
<td>0.012</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>Defoliation</td>
<td>-0.0041</td>
<td>0.033</td>
<td>NS</td>
</tr>
<tr>
<td><em>Patelloa pachypyga</em>:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aspen</td>
<td>Larvae</td>
<td>0.0094</td>
<td>0.036</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>Defoliation</td>
<td>0.0032</td>
<td>0.001</td>
<td>NS</td>
</tr>
<tr>
<td>Balsam</td>
<td>Larvae</td>
<td>-0.0016</td>
<td>0.046</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>Defoliation</td>
<td>-0.0333</td>
<td>0.044</td>
<td>NS</td>
</tr>
</tbody>
</table>

* 'NS' indicates P > 0.05.

aspen poplar leaves. Likewise, in field studies, more *L. exul* were observed landing on the tree canopies of aspen poplar trees containing FTCs as compared to balsam poplar trees with FTCs. Simple regressions indicated that as larval abundance increased on aspen poplar trees, so did fly attraction. This may reflect the correlation between larval abundance and the level of recent defoliation rather than of total defoliation, *per se*. It is unlikely that parasitoids were visually attracted to the caterpillars because the majority of the larvae were clustered on the tree trunks and in many cases were hidden by the canopy leaves of the tree. These larvae would not have been visible to the parasitoids until the flies had already entered the tree canopies. Locating areas with recent plant damage would ensure a reasonable chance of egg ingestion and resulting parasitism rates. Thus, using the FTC-aspen poplar complex as an attractive cue would result in a very successful method of host-finding.

Tachinids that oviposit on leaves, as far as is known, rely on the odor of damaged foliage to locate host larvae. *Cyzenis albicans* is attracted to odours from oak trees damaged by the winter moth *Operophthera brumata* (Roland et al., 1989; Roland et al., 1995). Many studies of host-finding by tachinid parasitoids, that directly attack host larvae, emphasize the importance of the larval food plants. *Drino bohemicus* and *Bessa harveyi* are attracted to insect-damaged foliage particularly on unhealthy plants (Monteith, 1964). *Lydella griseiscens*, a parasite of the European corn borer *Ostrinia nubilalis* is attracted primarily to corn plants and secondarily to the host insect feeding on corn (Franklin & Holdaway, 1966). Attack by *Eucelatoria bryani* is affected by variety, morphology, and phenology of plants fed on by its host *Heliothis* spp. (Martin et al., 1990). Although, some tachinids have been found to use other cues such as auditory (Cade, 1975), visual (Herrebout & van der Veer, 1969; Monteith, 1955; 1958), and vibration (Monteith 1956).

A more generalized host-finding pattern, similar to the one found for *L. exul*, has been found for many hymenopteran parasitoids. These parasitoids are attracted principally to the host-host plant complex, secondarily attracted to host produced compounds (e.g. frass), and least attracted to host insect odors. For example, female *Aphidius ervi* are attracted to the pea aphid (*Acyrthosiphon pisum*)-host plant complex, secondarily to the odor from previously damaged plants, and lastly to *A. pisum* (Du et al., 1996). *Cotesia rubecula* is attracted primarily to the *Pieris rapae*-host plant complex over artificially damaged leaves, secondarily to frass volatiles, and least to the host insect (Geervliet et al., 1994; Agelopoulos et al., 1995). To *Microplitis croceipes* both artificially damaged leaves and frass are attractive, but not as much as the *Heliothis zea*-cowpea (*Vigna unguiculata*) complex (Eller et al., 1988). This same pattern of attraction has been found for *Cotesia marginiventris* and the beet armyworm (*Spodoptera exigua*)-corn complex (Turlings et al., 1991), *Cotesia*
Field bioassays showed that more *P. pachypsyga* landed on the tree canopies of aspen poplar trees containing FTCs as compared to balsam poplar trees with FTCs. Unfortunately we were unable to perform laboratory bioassays with this fly species to clearly identify the stimuli attracting *P. pachypsyga* to its lepidopteran host. In field bioassays, variables such as defoliation and larval abundance did not contribute substantially to the variation in fly attraction. It may be that our observations were not detailed enough to identify the stimuli attracting *P. pachypsyga* to host larvae, or, like other tachinids mentioned above, this fly species may be attracted to odors given off by aspen poplar trees independent of larval cues. Only further experimentation on this fly species will help to identify the cues used for attraction to its FTC hosts.

Discovering the general cues used as attractants by these two species of tachinid flies is only a preliminary step in understanding the chemical ecology of how the flies locate their hosts, and help in understanding spatial variation in host mortality and dynamics.

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